

WARENDJA WAKEFIELDI, A NEW GENUS OF WOMBAT
(MARSUPIALIA, VOMBATIDAE) FROM PLEISTOCENE SEDIMENTS IN
McEACHERNS CAVE, WESTERN VICTORIA

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Abstract

Two mandibles and six isolated teeth recovered from Pleistocene sediments in McEacherns Cave, western Victoria, represent a new genus and species of a morphologically primitive wombat. It combines unrooted, slightly bilobed molars showing little curvature, with a slender ramus, unfused symphysis, weak development of the masseteric and pterygoid fossae, a low-set articular condyle, and a broad coronoid process. The associated faunal assemblage includes typical later Pleistocene taxa, such as *Zygomaturus trilobus*, *Sthenurus gilli*, *S. cf. occidentalis* and *Thylacoleo carnifex*. Modern taxa, dominated by *Rattus fuscipes*, *Antechinus stuartii* and *Perameles nasuta*, indicate wet sclerophyll forest conditions.

Introduction

McEacherns Cave lies about 550 m south of the Glenelg River, in the Lower Glenelg National Park, southwestern Victoria. In 1963, A. C. Beaglehole and F. Davies discovered fossil mammal bones in the cave and commenced preliminary excavations in the floor sediments. This work was continued in 1964 and 1965 by the late N. A. Wakefield, who carried out extensive excavations. In 1967, Wakefield published a preliminary report describing the cave and its sediments, and listing the faunal remains from the initial excavations in 1963 and 1964. The bulk of the material, only partly sorted, was deposited in the National Museum of Victoria in 1972, after Wakefield's death. In 1975, J. H. Hope commenced sorting the Wakefield Collection, and followed this by further excavations at McEacherns Cave in November-December 1977. In May 1978, the remains of a previously undescribed genus of wombat were found in the material from the 1964-5 excavation. The specimens have been registered in the palaeontological collection of the National Museum of Victoria.

Terminology and Measurements

Mandibular terminology follows Stirton (1967), and dental morphology Archer (1978). In this latter system, the permanent cheek teeth of vombatids are P3, M2, M3, M4 and M5. Measurements were made with a Mitutoyo dial caliper, to 0.1 mm.

Systematics

The following diagnoses are not intended to be exhaustive at each taxonomic level, but rather are restricted to those features which can be observed on the type and referred specimens of *Warendja wakefieldi*.

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTA Owen, 1866
Family VOMBATIDAE Burnett, 1830

Diagnosis: Distinguished from all other Marsupialia by the presence of four bilobed, hyposodont, labially curved and open-rooted molars and open-rooted I1 and P3.

Warendja gen. nov.

Type species: *Warendja wakefieldi* sp. nov.

Known distribution: Pleistocene, western Victoria.

Diagnosis: Distinguished from all other vombatids by small, sub-rectangular, minimally bilobed molars, which show little longitudinal curvature; smooth, unfused mandibular symphysis; the combination of a broad ascending ramus and well developed coronoid process with poorly-developed masseteric and pterygoid fossae; and the close approximation of the articular condyle to the plane of the mandibular tooth row.

Etymology: In the language of the Woiwuro people of the Melbourne district, *warendj* means wombat (Hercus, 1969).

Warendja wakefieldi sp. nov.

Plate 3, Figure 2

Holotype: NMV P48980, right mandibular fragment with P₃, M₂₋₅, and alveolus for I₁. The articular condyle is present but the upper portion of the coronoid process is broken away.

Referred specimens: NMV P48982, right mandibular fragment with P₃, M₂₋₅ and the basal portion of I₁. The articular condyle and part of the coronoid process are not preserved. NMV P48981, isolated right M₅. NMV P165428, isolated left I₁. NMV P165429, isolated left P₃. NMV P165430, isolated left M⁴. NMV P165431, isolated right M⁴. NMV P165432, isolated left M³.

Type locality: McEacherns Cave, Lower Glenelg National Park, western Victoria. The specimens were among material in the National Museum of Victoria derived from the sediments identified as Pleistocene by Wakefield (1967). P48980 was collected 21 December 1964, from level 'R', by N. A. Wakefield. P48982 was collected 4-5 September 1964, from a section 24 to 27 feet northwest of the cave entrance, 0 to 1 inch below 'ML', by N. A. Wakefield. P48981 was collected 22nd May 1964, from level 'B2' in a section 18 to 21 feet northwest of the cave entrance, by N. A. Wakefield. P165428-32 were collected from level 'Q', by N. A. Wakefield.

Diagnosis: That of the genus until other species are described.

Etymology: Named in honour of the late Norman Arthur Wakefield.

Description

Mandible: (Table 1): The mandible is remarkably smaller and more delicately built than in all other known vomatids. In P48980 especially, and to only a slightly lesser degree in P48982, this is emphasised by the swept-back appearance of the ascending ramus, the anterior border of which is inclined at a lesser angle than in any other described species. The lightly built appearance of the mandible is due to the presence of very shallow masseteric and pterygoid fossae, again a feature not found in any other wombat species.

When viewed laterally, the ventral border of the mandible forms a very shallow curve with a

TABLE 1
Measurements (mm) of the mandible of
Warendja wakefieldi

	P48980	P48982
Length of mandible	92.5	est. 100
Greatest width of mandible	21.5	21.2
Depth of ramus below mid M ₄	20.3	24.2
Length of diastema	16.8	16.9
Length from alveolus of incisor to posterior alveolar margin of M ₅	51.2	57.6
Width of ascending ramus	33.0	
Condyle—transverse width in vertical orientation	12.9	
maximum transverse width	14.1	
maximum length in antero-posterior direction	7.8	
Height from ventral border of ascending ramus to sigmoid notch	33.1	

concavity beneath the anterior root of the ascending ramus and a convexity beneath M₄. In both mandibles the symphysis is elliptical in shape. Its major axis is about 34 mm long in P48982 (the posterior end is broken in P48980), and in both specimens dips posteriorly at an angle of 30° with respect to the dorsal edge of the horizontal ramus. The length of the minor axis is 9.4 mm in P48980 and 10.8 mm in P48982. The surface of the symphysis is only slightly roughened in both specimens, and there is no indication of symphyseal fusion between left and right mandibles.

This condition could be taken as evidence that both mandibles were juvenile, but P48980 is certainly fully adult. A fortuitous break between P₃ and M₂ allowed inspection of the full length of these teeth, which have almost identical top and bottom dimensions. In juvenile wombats, all teeth are distinctly conical, with proximal dimensions greater than distal (wear surface). The disparity reduces progressively until adulthood is reached. P48982 is an older adult specimen, showing a greater amount of tooth wear. Therefore the lack of symphyseal fusion is a valid diagnostic character.

The diastema is simple in morphology and relatively short. In P48980 the diastemal margin is a sharp crest, folded inwards slightly, above a longitudinal groove on the labial surface of the ramus. P48982 is similar, but is not as well preserved. The mental foramen in P48982 is large, and lies below the anterior

alveolar edge of P_3 . In P48980 the mental foramen lies anterior to P_3 , below the diastema. A second, smaller foramen lies posterior to this, below the posterior half of P_3 .

In both mandibles the anterior root of the ascending ramus is opposite the posterior lobe of M_5 . Its anterior border sweeps back in a gentle convex curve. Although the top of the coronoid process is not preserved in either specimen, it is clear that it, and the ascending ramus, are larger relative to the postero-ventral width of the ramus than in any other wombat.

Angle a as defined in Figure 1 is 56° in P48980, and 59° in P48982. The condyle is preserved only in P48980. It is small and ovoid, its transverse width about twice its length antero-posteriorly. It is set very low, close to the plane of the tooth row, as indicated by a measurement of 18° for angle b as defined in Figure 1. The articular surface of the condyle is on the lingual side, approaching the line of the tooth row.

The masseteric fossa is well-preserved in both mandibles. It is very shallow in P48980, deeper in P48982. The deepest area of the concavity lies immediately behind the anterior border of the ascending ramus, indicating that the main area of insertion of the masseteric muscle was higher and more anterior than in other wombats. The posterior masseteric eminence is well developed in P48982, with a sharp up-turned edge; in P48980 this outer flange is smooth and weakly developed. There are two foramina within the masseteric fossa in P48982, but only one in P48980.

The pterygoid fossa is also very shallow for a wombatid. In P48980 it forms a shallow lateral concavity with no ventral floor, due to the lack of development of the lingual flange of the fossa. In P48982, this flange is better developed, and the fossa is deeper with a flat floor ventrally. The height of the ventral rim of the mandibular foramen above the ventral border of the horizontal ramus is 9.8 mm in P48980, and 10.1 mm in P48982. In P48980 this foramen is simple and rounded; in P48982 it is part of a large depression in the centre of the pterygoid fossa, and the bone posterior to it is fenestrated. In both mandibles the angular process is broken but in the better preserved

P48980 it probably did not extend as far as the most posterior point on the condyle.

There is no digastric fossa present on either mandible. Instead, the lingual surface of the horizontal ramus forms a smooth convexity, with its highest point immediately behind the posterior limit of the symphysis. This bulge is caused by the large open root of the lower incisor, which in P48982 can be seen through a break in the bone.

Dentition (Tables 2, 3): The total length of the molar row in the holotype P48980 is 32.5 mm (occlusal measurement), and the corresponding figure for the referred specimen P48982 is 37.8 mm. These figures are significantly smaller than for any other wombat currently accepted as a valid species. All the teeth are open rooted. As in *Vombatus* and *Lasiorhinus* there is no distinct cemento-enamel junction. The cementum continues over the enamel up the column of the tooth to the occlusal surface, so in most cases enamel is visible only as a rim at the occlusal surface. With isolated teeth, the distribution of enamel can be determined not only by its appearance at the occlusal surface, but by the presence of brown and white transverse markings, indicating zones of enamel formation, on the columns of the tooth, towards the root.

I_1 : The incisor is represented by a broken basal portion in P48982, and by an almost complete alveolus in P48980. In P48982 it is a simple, ovate tooth, much deeper than wide at its broken end. The alveolus in P48980 is similar in shape. The enamel is restricted to the ventral and lower labial surfaces. The open root extends back to beneath the mid-point of M_3 .

P_3 : The premolar is sub-triangular in occlusal outline, weakly bilobate, and has its long axis parallel to the antero-posterior axis of the mandible. It is slightly offset lingually to the molar row, and the posterior apex of the triangular occlusal outline is adpressed against the antero-lingual corner of M_2 . In P48980 the tooth is nearly vertical, but in P48982 it is curved antero-posteriorly. Enamel is restricted to the anterior rim of the anterior lobe of P_3 in P48980; in P48982, enamel occurs only on the anterior labial surfaces of both the lobes. There

TABLE 2

Measurements (mm) of lower teeth of *Warendja wakefieldi* (occlusal, unless otherwise stated)

	P48980	P48982
Total length P ₃ -M ₅	32.3	37.8
Total length P ₃ -M ₅ †	35.5	40.8
P ₃ length	5.3	6.6
width of anterior lobe	2.4	2.9
width of posterior lobe	3.1	3.7
height above alveolar margin of posterior crest	4.0	6.1*
height above alveolar margin of notch	2.2	5.3
difference in elevation between notch and posterior crest	1.8	0.8
M ₂ length	7.4	8.2
width of anterior lobe	3.9	4.7
width of constriction	3.5	4.6
width of posterior lobe	5.1	5.6
height above alveolar margin of crest of anterior lobe	4.4	9.3
height above alveolar margin of posterior lobe	2.5	6.2
difference in elevation between upwards projection of anterior lobe, and occlusal surface of the posterior lobe	2.3	3.1
M ₃ length	7.4	8.6
width of anterior lobe	4.4	5.5
width of constriction	4.2	5.2
width of posterior lobe	5.5	6.2
M ₄ length	6.8	8.7
width of anterior lobe	5.0	5.8
width of constriction	4.0	5.0
width of posterior lobe	4.8	6.0
M ₅ length	6.0	7.4
width of anterior lobe	4.2	5.1
width of constriction	3.7	4.8
width of posterior lobe	4.0	4.8
I ₁ width	5.2†	5.5
depth	8.3†	8.0

* Not strictly comparable to P48980 because alveolar margin appears to be more broken away.

† Alveolar measurements.

is a distinctive pattern of wear on both premolars. In P48980 this has resulted in a deep notch on the occlusal surface running diagonally from antero-lingual to postero-labial, leaving the anterior and posterior rims of the tooth standing as sharp crests. In P48982, at a later stage of tooth-wear, the occlusal surface is saddle-shaped, with the enamel-less posterior rim left as a sharp point.

M₂₋₅: The occlusal outline of all the molars is sub-rectangular, with slightly developed, but

TABLE 3

Measurements (mm) of isolated teeth of *Warendja wakefieldi* (occlusal, unless otherwise stated)

I ¹ (P165428)	
depth at proximal end of wear facet	5.9
width at proximal end of wear facet	4.0
depth at open root	5.4
width at open root	3.7
length of wear facet	9.2
width of wear facet	3.9
P ³ (P165429) length	6.4
width of anterior lobe	4.0
width of posterior lobe	4.5
M ⁴ (P165430) length	7.7
width of anterior lobe	6.5
width of constriction	5.2
width of posterior lobe	6.2
M ⁴ (P165431)	
width of anterior lobe	6.5
M ³ (P165432) length	7.8
M ₅ (P48981) length	5.6
width of anterior lobe	4.3
width of constriction	4.1
width of posterior lobe	4.9

distinct bilobation. The lobes are almost quadrangular in cross-section, with rounded corners. A thin rim of enamel extends around the lingual and labial edges of the occlusal surface of the teeth. It is absent anteriorly and posteriorly on each tooth. The anterior lobe of M₂ is narrower than the posterior, which is the most nearly cylindrical of any lobe of the four molars. The anterior lobe of M₂ is distinctly smaller in both length and width. It is also distinguished by a peculiar wear pattern, related to that of the premolar. Whereas the occlusal surfaces of M₃₋₅, and of the posterior lobe of M₂, are nearly horizontal, the occlusal surface of the anterior lobe of M₂ rises anteriorly at a sharp angle. When viewed laterally, the anterior lobe of M₂ in P48982 protrudes as a sharp, high crest from the nearly horizontal occlusal surface of the tooth row. In P48980 the equivalent high crest is made up of both the anterior lobe of M₂ and the posterior lobe of P₃.

In common with other vombatids, M₃ is the widest molar, its posterior lobe being the widest part of the molar row. The lobes are more nearly equi-dimensional than those of M₂, and the occlusal outline is almost subrectangular.

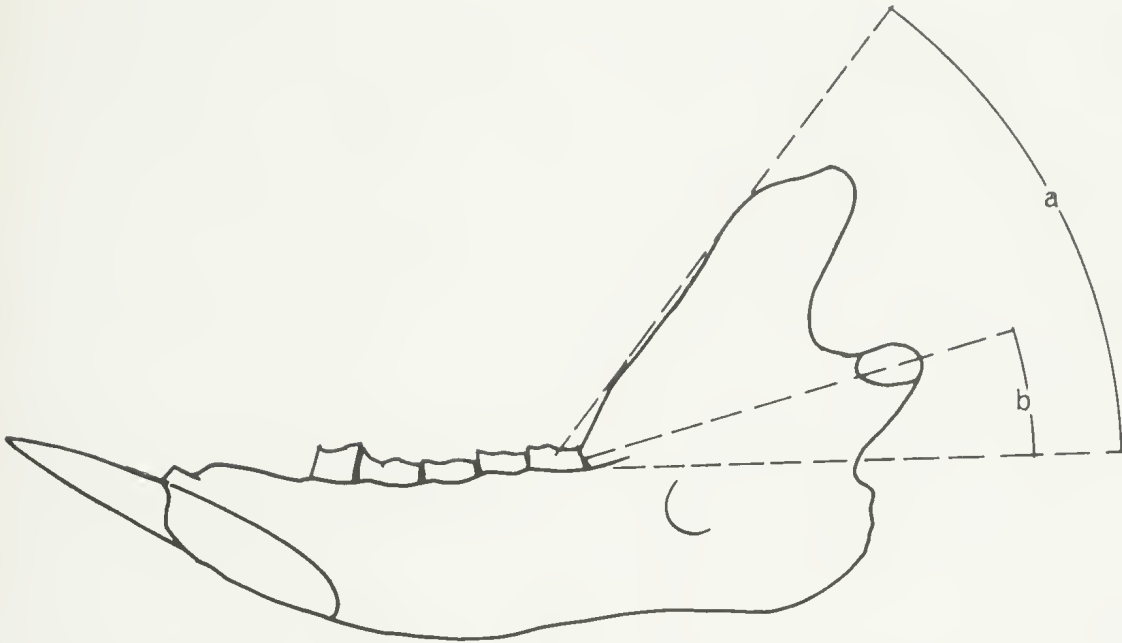


Fig. 1. Schematic diagram of the mandible of *Warendja wakefieldi* illustrating the method of measuring inclination of anterior border of ascending ramus (angle a) and elevation of condyle (angle b).

The anterior lobe in both specimens retains a trace of a transverse loph on the lingual side, and this is also visible on the anterior lobes of M_4 and M_5 in P48982. In M_4 the two lobes are nearly equal in size and the tooth is the most nearly rectangular of all the molars. The last molar, M_5 , is the smallest, and tapers markedly posteriorly. The isolated tooth, P48981, appears to be a right M_5 , in showing the bilobed form characteristic of the molars, but with one lobe clearly smaller than the other. It is most similar to M_5 of P48980. Wear on M_{3-5} is transverse and has left the lingual rim of the molars standing higher than the labial rim.

The remaining five isolated teeth are interpreted as representing elements of the upper dentition.

I^1 : A left upper incisor, P165428, is attributed to *Warendja* because of its open root, but smaller size and different morphology from any other wombat. The tooth is longitudinally curved, laterally compressed and ovate in cross-section. It tapers slightly from the distal to the proximal end. Enamel occurs on the anterior

(dorsal) and labial faces. There is an elongate, ovate wear surface on the posterior face of the tooth. The occlusal surface is slightly asymmetrical, being flattened on the lingual side, where it abuts the right incisor.

P^3 : A single tooth, P165429, is tentatively identified as a left upper premolar. It is similar to the lower premolars in being longitudinally, rather than laterally curved (as the molars are), and in having an extensive exposure of enamel on the convex (anterior) face. It is, however, larger and more ovate than the lower premolars. It is bilobed, with the labial groove deeper than that on the lingual face. The depth of enamel on the anterior face is 5.5 mm below the occlusal surface. Enamel extends onto the labial and lingual faces of the anterior lobe, and also occurs on the antero-labial face of the posterior lobe.

The upper premolar should occlude with both P_3 and the anterior lobe of M_2 . In both lower dentitions available, differential wear has occurred on the anterior teeth, leaving the anterior lobe of M_2 standing as a high crest. This suggests that the upper premolar occludes mainly with the lower, and that there is minimal wear on the anterior lobe of M_2 , except at the posterior of this lobe, where it meets M^2 . The

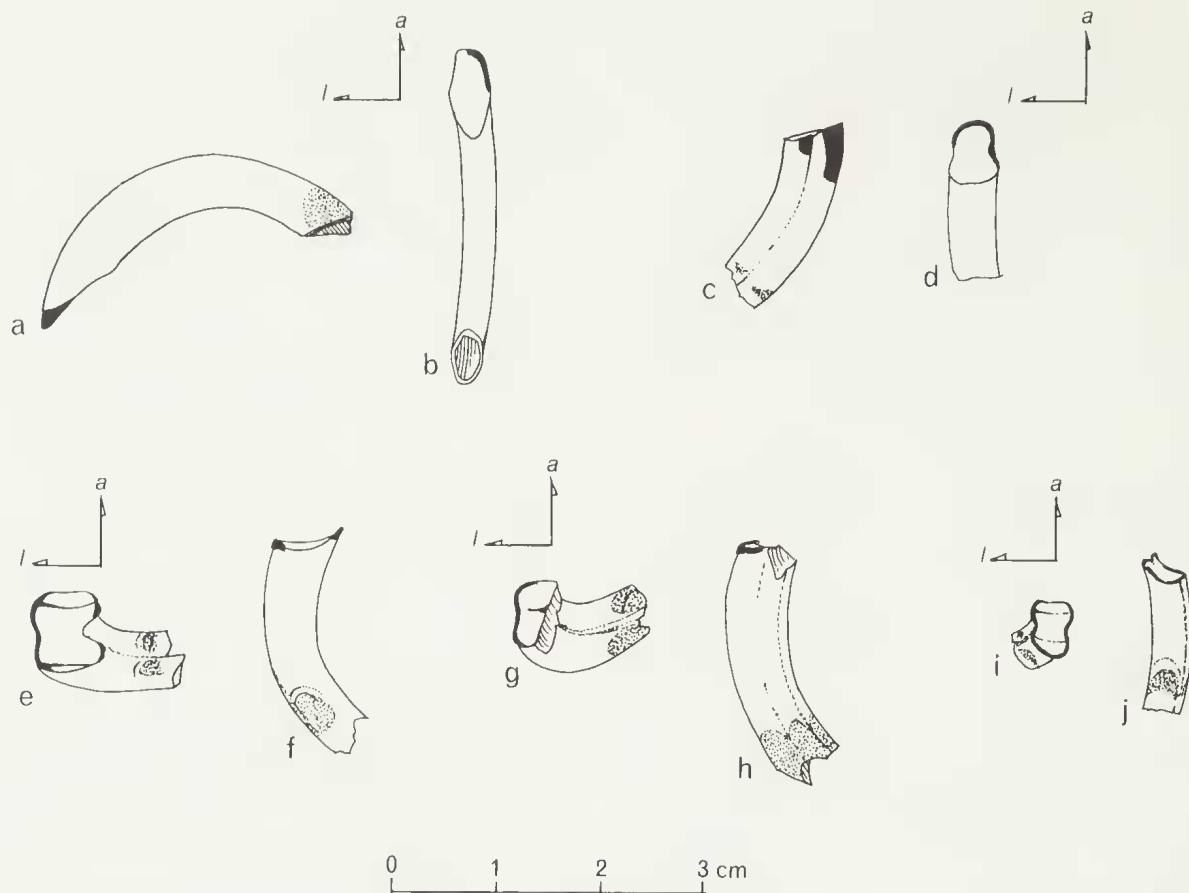


Fig. 2. Isolated teeth of *Warendja wakefieldi*. NMV P165428, left I¹, a, labial view; b, occlusal view. NMV P165429, ? left P³, c, labial view; d, occlusal view. NMV P165430, ? left M⁴, e, occlusal view; f, posterior view. NMV P165432, ? left M³, g, occlusal view; h, posterior view. NMV P48181, right M₅, i, occlusal view; j, posterior view. Orientation of occlusal views; a-anterior, l-lingual.

occlusal surface of P165429 shows a saddle-shaped wear pattern similar to that of the lower premolars, but less extreme. The wear is consistent with the argument that P³ occludes mainly, or only, with P₃, but a complete maxillary tooth row, with associated mandible, would be needed to verify this.

Upper molars: Three isolated molars are attributed to *Warendja* on the basis of size, and their minimal degree of bilobation and curvature. They are larger than the lower molars, have an asymmetric occlusal outline, and are more strongly curved, so are interpreted as upper molars.

On the assumption that the concave face of

each upper molar is labial, as in other vomobatids, then the labial and lingual orientations are easily determined. The allocation of each tooth to left or right, or to specific positions in the tooth row, is tentative, and has been based on the direction of curvature of the roots, by comparison with *Vombatus* and *Lasiorhinus*.

These molars are distinguished by the asymmetry of their medial constriction. The lingual (convex) face is barely constricted, with a shallow indentation running the length of the root. The lingual enamel surface is virtually uninflected. In contrast, the labial (concave) surface is more deeply constricted, to the degree found on both labial and lingual faces of the lower molars.

As in the lower molars, enamel is restricted to the labial and lingual surfaces of the teeth. In the only unbroken specimen, P165430, the labial edges of the anterior and posterior lobes form sharp points, although this is more the result of wear than of the structure of the tooth.

Wear has left the labial rim of the tooth standing higher than the lingual rim. In P165430 traces of transverse lophs can be seen on the occlusal surface of the anterior and posterior lobes.

Discussion

The taxonomy of wombats at the generic level has been in a state of flux for many years. One of us (HEW) presented a phylogeny of the family at the 1971 Brisbane ANZAAS, but circumstances have so far prevented publication of this work, which was based on a comprehensive study of virtually all fossil wombat material available in Australia at that time. The most recent published consideration of wombat phylogeny is that of Dawson (1981), who recognised the following Pleistocene and modern taxa: *Vombatus ursinus*, *Phascolonus gigas*, *Ramsayia magna*, *Lasiorhinus medius*, and *Lasiorhinus latifrons*, and suggested that the recently described *Phascolonus lemleyi* Archer & Wade 1976 should be referred to *Ramsayia*. In addition to the above, Wilkinson (in prep) recognises *Vombatus hacketti*, *Lasiorhinus krefftii* and *Phascolonus angustidens* as valid species of true wombats, and regards the generic status of *medius* as problematical. *Rhizophascolonus crowcrofti* is the only described vombatid genus restricted to the Tertiary (Stirton et al. 1967), but this differs from all other vombatids in having a rooted premolar.

Dawson's phylogenetic scheme is at considerable variance with that put forward by Wilkinson (1971), in prep), on which the discussion below is largely based. However, the alternative views put forward by Dawson are also referred to.

Generic status for *Warendja wakefieldi* is justified by the so far unique combination of the open-rooted, hypsodont teeth, with the gracile mandibular morphology. The teeth, clearly vombatid in form, differ from all known vombatids in their minimal curvature, and their weakly bilobed morphology. The lower premolar shows some similarity to those of *Phascolonus* and *Ramsayia*, particularly in the antero-posterior orientation, incipient bilobation and size, relative to the molars, but differs

in being sub-triangular in occlusal outline rather than ovoid to sub-rectangular. There is little affinity with the ovoid, more or less obliquely set lower premolars of *Lasiorhinus* and *Vombatus*.

The sub-rectangular, sub-bilobate molars differ from all other wombats in their distinctive occlusal outline and small degree of longitudinal curvature, but are closest to *Phascolonus* and *Ramsayia* in general appearance. The most noticeable differences between *Phascolonus* and *Warendja* are the relatively small degree of medial constriction and the less rounded angles of the molars in the latter. It is easy to envisage an evolutionary trend from the *Warendja* molar type to that of *Phascolonus* by an increase in medial constriction, and an increase in rounding of the lobes to give a more cylindrical appearance. There is no close affinity to the rounded triangular lobes of *Lasiorhinus* molars, and even less to the sharply angled lobes of *Vombatus* molars.

The single tooth, considered to be a P₃, representing the Miocene genus *Rhizophascolonus*, differs from all known wombats, including *Warendja*, in having closed roots. Although not directly comparable with *Warendja*, as illustrated in Stirton et al. (1967), it does show some similarity to the molars of *Warendja* in the rounded cylindrical form of the lobes. The simple cylindrical lower incisor of ovoid cross-section is very similar to that of *Phascolonus angustidens* (Wilkinson, in prep.), and is also similar in both shape and the extent of surface enamel to *Phascolonus gigas*, and especially to *Ramsayia* (Dawson 1981, Wilkinson in prep.). The upper incisor is also simple and is quite distinct from the broad flattened upper incisor of *Phascolonus gigas*.

The larger of the two mandibles (P48982) is fully adult, so *Warendja wakefieldi* is considerably smaller than any of the described wombat species. The nearest in size is the small Bass Strait Islands wombat, *Vombatus ursinus*, but this is a scaled down version of the common wombat of southeastern Australia, *Vombatus hirsutus*, which is regarded by some authorities (e.g. Dawson 1981) as a sub-species of *ursinus*. Even if *ursinus* is accepted as a valid species, it is still larger than *W. wakefieldi*.

The detailed morphology of the mandible of *Warendja* reflects this small size. The slender jaw has shallow masseteric and pterygoid fossae, and a small articular condyle, compared with the deep pterygoid fossae, deep to very deep masseteric fossae, and wide, robust articular condyles in other vombatids. In *Phascolonus* and *Ramsayia* the mandible is very robust, but deep and comparatively narrow. In *Lasiorhinus* and *Vombatus* the mandible is very broad, with thick, relatively shallow rami, which support very powerful musculature. *Warendja* differs from all of these in the delicate build of the mandible and the lesser development of the masseteric and pterygoid fossae. While this light build is to some extent probably just a reflection of small size, two features of the mandible are especially un-wombatlike. The size and smoothness of the mandibular symphysis indicate that the left and right mandibular rami never fused, as happens in other wombats. The extremely low position of the articular condyle relative to the plane of the molar row is unique in vombatids, and indeed unusual compared with most other diprotodont families (Table 4).

In general, the articulation of the jaw tends to be in line with the tooth row in carnivores, but is much higher than the tooth row in herbivores. The high position increases the lever arm of the masseter muscle. The low angle in *Warendja* is more comparable to that found in carnivores, such as *Sarcophilus*, *Dasyurus* and *Thylacoleo* (Finch 1971), rather than herbivores. The only diprotodont groups which exhibit a low-set condyle are the phalangerids and potoroines. The jaw structure in rat-kangaroos such as *Aepyprymnus* and *Bettongia* differs in other ways from that in *Warendja*. The phalangerids, *Phalanger* and *Trichosurus*, are quite similar, however, not only in the position of the condyle, but in the relative proportions of the masseteric and pterygoid fossae and the ascending ramus. A comparative study of the jaw mechanics of these taxa might elucidate the feeding habits of *Warendja*.

These characteristics of the mandible of *Warendja* indicate a very different system of jaw musculature from other wombats, and this has implications for the structure of the as yet

TABLE 4

Comparative measurements of the angle of inclination of the ascending ramus (angle a) and of the elevation of the condyle (angle b). Angles approximate only

Taxon	a	b
VOMBATIDAE		
<i>Warendja wakefieldi</i>		
NMV P48980	56°	18°
NMV P48982	59°	—
<i>Vombatus ursinus</i>	70°	30°
<i>Lasiorhinus latifrons</i>	65°	35°
<i>Phascolonus gigas</i> ¹	75°	40°
DIPROTODONTIDAE		
<i>Raeneotherium yatkolai</i> ²	62°	<34°
<i>Diprotodon opatum</i>	105°	65°
PHASCOLARCTIDAE		
<i>Phascolarctos cinereus</i>	75°	38°
PHALANGERIDAE		
<i>Trichosurus vulpecula</i>	65°	28°
<i>Phalanger orientalis</i>	58°	10°
PETAURIDAE		
<i>Pseudocheirus peregrinus</i>	75°	38°
MACROPODIDAE		
<i>Bettongia lesueur</i>	55°	25°
<i>Aepyprymnus rufescens</i>	57°	22°
<i>Wallabia bicolor</i>	90°	40°
<i>Macropus giganteus</i>	75°	40°
THYLACOLEONIDAE		
<i>Thylacoleo carnifex</i> ³	35°	10°
PERAMELIDAE		
<i>Isodon obesulus</i>	60°	30°
<i>Perameles nasuta</i>	48°	30°
DASYURIDAE		
<i>Dasyurus maculatus</i>	60°	12°
<i>Sarcophilus harrisi</i>	62°	10°

¹ Measured on Plate XL, Stirling (1913).

² Figures quoted from Rich *et al.* 1978.

³ Relative to occlusal plane of P₃.

unknown skull of *Warendja*. By analogy with the skulls of *Trichosurus* and *Phalanger*, *Warendja* is likely to have had a more rounded cranium, with greater areas for insertion of the temporal muscles than in other wombats, and possibly some development of a sagittal crest. In *Vombatus* and *Lasiorhinus*, the structure of the zygomatic arch is distinctive, with no development of the masseteric process, but rather a broad area excavated beneath it for the insertion of the masseter muscle. Given the probable lesser development of the masseter in *Warendja*, the structure of the zygoma may have been more like that of the phalangerids,

with the anterior zygomatic surface vertical rather than horizontal (as in other wombats), and with a masseteric process. In summary, the skull of *Warendja* will probably look more like that of *Trichosurus* than any wombat. This is not to imply any special relationship between phalangerids and *Warendja*; these characters are probably plesiomorphic for diprotodonts generally.

Dawson (1981) carried out a cladistic analysis of the five vombatid taxa she recognised, using a set of seven dental and palatal characters. The resulting cladogram linked *Vombatus ursinus* with *Phascolonus gigas*, and *Ramsayia magna* with *Lasiorhinus latifrons* and *L. medius*. For most of Dawson's dental characters, *Warendja* exhibits the plesiomorphic state. The one exception is the depth of the lower incisor, where the apomorphic state, I_2 being deeper than wide, is found in *Warendja*. *Warendja* is intermediate with regard to the structure of the lower premolar, but Dawson concluded that convergence had occurred in this character among vombatids. Dawson's cladistic analysis does not clarify the relationship of *Warendja* to other vombatid taxa, since it is plesiomorphic in most observable characters.

Warendja fits rather better into the as yet unpublished phylogenetic scheme of Wilkinson (1971; in prep). As shown above, it is linked to the *Phascolonus-Ramsayia* group by premolar and molar morphology, and more particularly by the morphology of the lower incisor. It has almost nothing in common with either *Lasiorhinus* or *Vombatus*, apart from family characters. The suggestion by Dawson that these latter genera have evolved separately, and gained similarity by convergence, cannot be sustained when skeletal characters are considered. The skulls of *Vombatus* and *Lasiorhinus* are basically similar, but readily distinguished, as are the skeletons of *V. ursinus* and *L. latifrons*. However, the skeleton of *L. krefftii* blurs the generic boundary to a remarkable degree, which is more readily explained by common ancestry than by convergence.

Warendja probably represents an ancestral vombatid type, from which the *Phascolonus-Ramsayia* group evolved. '*Phascolomys*' *medius* (whose generic assignment is prob-

lematical) is the link between *Phascolonus-Ramsayia* and *Lasiorhinus*, from which *Vombatus* has in turn been derived. In the light of this, the provenance, probable age and faunal association of *Warendja* are of especial interest.

Age and Palaeoenvironment

McEacherns Cave is formed in the Gambier Limestone, of Oligocene-Miocene age. It is approximately 60 m long, along a NW-SE axis, averages 3 m in width and 3 m in height and is connected to the surface by a vertical shaft 13 m deep and 1.5 m in diameter. The cave fill consists of sandy fossiliferous units and extensive roof-fall. The cave itself and the early excavations of the fossil-bearing sediments, in the northwest chamber of the cave, are described by Wakefield (1967) and Link (1967).

Wakefield recognised a series of stratigraphic units in the sandy floor sediments. The oldest of these, which he called the 'Pleistocene' sediments, consist of a block of compacted grey sands laid down on limestone boulders, part of an earlier roof-fall. Overlying this block is a 'calcarenite' deposit, about 5-10 cm thick, consisting of finely laminated layers of calcium carbonate beneath 5-20 cm of grey clay. Above and on each side of the block of grey sand with its calcarenite capping are successive layers of white, red and black sands, Wakefield's 'Recent' sediments. Laterally the white sands are in fact at a lower level than the grey block, filling a cavity formed by slumping and collapse.

The new excavations by Hope at McEacherns Cave confirm this basic stratigraphy, although some details are at variance with Wakefield's report, and the stratigraphy of his 'Recent sands' is probably more complicated than he recognised.

Wakefield obtained only one radiocarbon date from the site based on 373.4 g of mammal bones extracted from the uppermost layers of the grey block, about 0.5 cm below the calcarenite layer. This material gave a date of $15,200 \pm 320$ years before present (GaK-509). This date for the top of the grey sand, along with the absence of any element of the extinct Pleistocene fauna from the overlying white and red sands (except as reworked material) was in-

terpreted by Wakefield as indicating that the older grey sand was late Pleistocene in age, while the remaining sediments were all Holocene in age. He suggested that the calcarenite layer indicated a period of aridity, attributed to 'a mid-Holocene warm-arid period'. Link (1967), however, argued that the calcarenite might have been formed by frost brecciation of the walls of the cave during an arid and possibly cold phase about 8-11,000 years before present.

The results of the 1977 excavations at McEacherns Cave suggest that the sedimentary sequence is in fact much older. Preliminary radiocarbon dates indicate that the younger sands were deposited between 15,000 and 2000 years before present. A sample of the laminated calcarenite layer has also been dated, and this gave an age of $28,580 \pm 850$ years (ANU-2030). It was expected that this date might be similar to Wakefield's original date of 15,200 years before present on bone from immediately under the calcarenite layer, on the grounds that since the bone date was likely to be affected by contamination, the calcarenite and bone carbonates might have equilibrated.

It has proved difficult to obtain suitable charcoal from the older grey sand for dating. One sample has given a preliminary date of about 24,000 years before present (ANU-2372), but given the reversal between this and the calcarenite date, it is likely that some as yet unclear source of contamination is affecting organic materials in this unit.

There is some circumstantial evidence to suggest that the grey sands may be considerably older than the last Pleistocene glaciation and thus probably beyond the range of radiocarbon dating. There is clear evidence in the excavated section that the grey block is in effect a residual, left stranded after a period of collapse, and subsequently surrounded by the younger sediments. Elsewhere in the cave, remnants of similar sediments containing a similar fauna, including extinct species, are plastered on the cave walls up to 3 m above the top of the grey block. The exact relationship of these sediments to the grey block cannot yet be determined, but they may relate to the same event of cave fill, most of which has now disappeared.

A considerable period of time must be allowed for the almost complete filling of the cave by the older sediments, the deposition of the laminated calcarenite layer, and for the subsequent removal of much of these sediments, before the younger phase of deposition began, sometime before 15,000 years ago. Further, given the relative positions of the remnants of the older sediments, the excavated block of grey sediment may in fact date from the earlier stages of the older depositional event. An absolute age for the grey sediments is likely to prove impossible to obtain, but a hypothetical age for the calcarenite deposit and the sediment removal can be suggested, on the assumption that these are related to changes in regional watertable.

During the last interglacial maximum episode, from about 135-120,000 years ago, the maximum sea level relative to the New South Wales coast is considered to have been 5 ± 1 m above present sea level (Chappell and Thom 1978). In western Victoria, high sea level stands of approximately the same magnitude, 7.5 m and 4 m (the later regarded as a stage during the retreat of sea level), are also attributed to this time period (Gill and Amin 1975). Interstadial high sea levels younger than 118,000 years are thought to have been at least 8 m lower than the 135-118,000 year levels (i.e. below present sea level) (Chappell and Thom 1978).

McEacherns Cave lies approximately 550 m south of the Glenelg River, which is tidal at this point, and the surface of the younger cave deposit is approximately 6 m above the present river level. Therefore during the last interglacial maximum, the lower levels of the sediments in the cave were likely to have been affected by a higher regional watertable, related to the higher sea level.

Corroborative evidence may come from a study of the calcarenite sediments, whose origin is unclear at the moment. Wakefield suggested that they were of aeolian origin, while Link proposed frost action; a further possibility is that they were laid down under standing water. If in fact the formation of the calcarenite layer and the subsequent roof-fall and removal of much of the older fill were related to the rise

and then lowering of the watertable, then these events may have occurred during and at the end of the last interglacial, 135-118,000 years ago. The grey sediments themselves would be even older.

The specimens of *Warendja wakefieldi* were found among the material from McEacherns Cave in the N. A. Wakefield Collection at the National Museum of Victoria. Some of this material is poorly documented and is difficult to attribute with absolute confidence to a particular stratigraphic layer. In 1964-5 Wakefield excavated five 3 ft wide sections from wall to wall across the width of the cave. These together extended from 15 ft to 30 ft from the cave entrance, and were numbered accordingly in 3 ft blocks, i.e. 15-18 ft, 18-21 ft etc. Most of the material collected during this phase of the excavation was labelled with the section numbers, and also with the depth from the surface, but no record was kept of the lateral position across the cave. Part of the collection, however, was labelled using a code of letters or numbers. Bones so labelled can be allocated a stratigraphic position only by comparison of colour, preservation and faunal composition with better documented material.

One specimen of *Warendja*, P48982, is clearly provenanced within the system. This is labelled '24'-27', 0"-1" below ML' (ML middle layer = calcarenite layer). Unfortunately it is not possible to allocate the remaining specimens to specific positions in the excavation. The colour and degree of mineralisation of all specimens, and of the rest of the bone material with which they are associated, indicates that they are derived from the older Pleistocene unit.

Wakefield (1967) lists the faunal assemblages recorded from the older Pleistocene sediments, and from the younger Pleistocene red and black sands, based on material collected during the initial excavations in 1963 and 1964. He interpreted the faunal sequence from the younger sands (now known to be from more than 15,000 to about 2000 years before present) as indicating a change from a 'mallee' fauna, through a fauna including some woodland species, to the modern dry sclerophyll forest of the district.

In the older Pleistocene sediments the faunal assemblage is dominated by *Rattus fuscipes*, *Antechinus stuartii*, *Perameles nasuta* and the extinct kangaroo *Sthenurus gilli*. Other extinct Pleistocene species present are *Sarcophilus lamiaris*, *Zygomaturus trilobus*, *Thylacoleo carnifex*, *Sthenurus* cf. *occidentalis* and *Proteunodon* cf. *brehus*. *Vombatus* sp. also occurs in the assemblage, but only isolated teeth have so far been recovered. Notable by their absence are many elements of the modern woodland and heath communities, such as *Antechinus swainsonii*, *Sminthopsis* cf. *leucopus*, *Isoodon obesulus*, *Trichosurus vulpecula*, *Macropus rufogriseus*, *Conilurus albipes* and *Pseudomys shortridgei*, all of which are abundant in the younger sediments in the cave. Preliminary analyses of the material collected by Wakefield in 1964-65, and by Hope in 1977 support these faunal lists for both the older and younger sediments.

Wakefield interpreted the faunal association from the older Pleistocene sediments as indicative of wet sclerophyll forest, which today occurs in areas of Victoria with an annual rainfall of 1000-1200 mm or more, such as the Otway Ranges and the east-central highlands. The dramatic change in faunal composition between the older and younger sediments also supports the hypothesis of a long hiatus in sedimentation within the cave.

Conclusion

Warendja wakefieldi is an enigma. The open-rooted dentition is clearly vombatid, but it combines some characters that could be seen as plesiomorphic, such as the minimally bilobed form of the molars, and the extent of enamel on I_1 , with others, such as the grooving on P_1 and the depth of I_1 , which could be regarded as apomorphic. The mandible is unique in vombatids, and bears more resemblance to that of phalangerids. It probably represents a plesiomorphic diprotodont morphology.

It would have been no surprise if *Warendja wakefieldi* had turned up in a Miocene site, where its small size and primitive features would have conveniently fitted it for the role of ancestral wombat. *Warendja*, however, has been found in terrigenous sediments within a

cave eroded in Miocene limestone, in association with typical Pleistocene and modern species. Although circumstantial evidence suggests that the sediments from which *Warendja* comes may be older than 120,000 years, there is no reason to suppose they are significantly older, say, of early Pleistocene age. So far, *Warendja* is the only taxon recognised in the site which has not been found elsewhere in Victoria in a late Pleistocene context.

The palaeoenvironment suggested by the faunal assemblage associated with *Warendja* is wet sclerophyll forest. The suite of modern species in the assemblage occurs in such forest in Gippsland today. *Warendja*, with its primitive morphology, may be a conservative survivor from the forests of the Tertiary, lingering into the Pleistocene in the forested areas of southeastern Australia.

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Explanation of Plate

PLATE 3

Warendja wakefieldi. NMV P48980, holotype, right mandible, McEacherns Cave, Victoria, fig. 1, labial view, $\times 1$; fig. 2, lingual view, $\times 1$; fig. 5, occlusal view, $\times 1$. NMV P48982, right mandible, McEacherns Cave, Victoria, fig. 3, labial view, $\times 1$; fig. 4, lingual view, $\times 1$; fig. 6, occlusal view, $\times 1$.

